

THE PHYTOGEOGRAPHY OF MOLLUGINACEAE WITH REFERENCE TO SOUTHERN AFRICA.

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ABSTRACT.

All the genera are essentially southern in distribution and suggest an origin in lands to the south of the Tethys Sea.

The distribution patterns are of two kinds, the one tropical and for the most part widespread, the other more southern and in most cases restricted and rather discontinuous. This separation appears to lend support to the expressed view that in Africa there was an early differentiation into types of flora, the one tropical and occupying the warmer and generally less elevated places, the other more temperate and found in cooler or more elevated regions. These two are referred to briefly as the "old tropical" and "old temperate" floras (cf. Boughey 1951).

Though this separation into the old tropical and old temperate floras is convenient and does appear to provide some explanation of features of distribution, it must be emphasized that any existing descendants must be extremely different from the originals which were much less diversified. All the existing floras have undergone prolonged development and differentiation. Even though some of the genera have the features of age, all exhibit greater or less evidence of continued species differentiation. In some, this has even been enough for separation of genera, as *Coelanthum* and *Polpoda*.

Again, during the course of evolution there must have been some overlapping of these old floras and penetration by elements of one into the territory of the other. This would be especially to be expected in plants such as these so many of which are characteristic of open ground and relatively low altitudes. Examples of this sort of thing in more recent times are found in the southward spread of species of *Mollugo*, in the spread of the karoo area of species of *Hypertelis* and *Pharnaceum*, and of *Limeum africanum* to the Cape region.

Descendants of the old temperate flora, to which most of the genera found in Southern Africa are to be assigned, are to be found in the Cape flora in the extreme south and south-west and in a number of patches on mountains especially in the east. There are also many stations for characteristic plants in sites where they are associated with plants derived

from other floras. All these evidently represent fragments of a once much larger area occupied by this kind of flora. The total range must have been of an extent sufficient to have given continuity between the existing fragments and stations. The main factor causing the reduction and break-up of area has been drying of the climate. Such reduction has brought about complete elimination of the old flora over wide areas and almost certainly the extinction of numbers of species though species differentiation has continued in the surviving parts, especially in the Cape region itself. The distribution patterns of the genera are the resultant of these various features, reduction in range, local survival and species development, all in a drying climate. The distribution does not give any evidence of directional migration.

It is worthy of note that in the course of these changes and restrictions some species surviving have remained unchanged while others have become modified. An example of the first is seen in *Psammotropha myriantha* which is found in very widely separated stations. The same is the case in *Hypertelis Bowkeriana*. On the other hand, the isolated species of *Pharnaceum* are specifically distinct.

Similar if less obvious changes have occurred in the descendants of the old tropical flora. The most striking case is that of *Limeum* where there has been great contraction and break-up of the one-time range.

The differentiation of the genera would seem to have taken place at a very early period, certainly previous to the restriction of the temperate flora. There are of course exceptions in the locally differentiated genera. Again, the more temperate genera are not closely allied to those in the tropics; all of them can best be looked upon as part of the old and now much reduced temperate flora.

The geographical, historical and other relationships of the various floras in Africa have presented problems for phytogeographers which have been much discussed but which cannot be looked upon so far as resolved. Indeed, the conclusions that have been drawn are often conflicting.

In these discussions the relationships of the rather unique Cape flora, which occupies the south-west corner of the continent, have figured rather prominently. This flora, which is regarded by all writers as an ancient one, is very distinctive and not closely allied to any other. With a view to the possibility of shedding some light on some aspects of the problems involved, this study of a group which is closely associated with the Cape

flora but by no means confined to it has been undertaken. The group chosen is one, *Molluginaceae*, which was raised to family rank by Hutchinson (Fam. Fl. Pl. ed. 1, 188, 1926; ed. 2, 857, 1959) but has generally been treated as a subdivision of the larger family Ficoidaceae (Aizoaceae) (e.g. Benth. & Hook. Gen. Pl. 1, 857, 1863; Engl. & Prantl Nat. Pflzf. ed. 1, 3.1 b, 1889; ed. 2, 16c, 1934).

The group comprises 13 genera which form a natural assemblage of herbaceous plants for the most part characteristic of dry or open situations but not especially succulent. The genera are: *Adenogramma* Reichb., *Coelanthum* E. Mey. ex Fenzl, *Corbichonia* Scop., *Gisekia* L., *Glinus* L., *Glischrothamnus* Pilger, *Hypertelis* E. Mey. ex Fenzl, *Limeum* L., *Macarthuria* Hueg., *Mollugo* L., *Pharnaceum* L., *Polpoda* Presl and *Psammotropa* E. & Z.

All these genera exhibit certain features in common, but some are more nearly inter-related and seem to represent lines of evolution within the group. Of such subgroups the largest comprises *Mollugo*, *Pharnaceum*, *Coelanthum* and *Hypertelis*. Of these, *Mollugo* seems the least specialized in habitat, habit and in floral structure. It has also the widest geographical range and seems probably the most primitive. *Pharnaceum* is very closely allied but is more specialized in habit, in inflorescence, and in floral structure. *Coelanthum* seems undoubtedly a local derivative from *Pharnaceum*. *Hypertelis* appears to be derived from the same stock, though not very closely allied. It has become specialized in habit, inflorescence and in habitat requirements.

The three genera, *Psammotropa*, *Polpoda* and *Adenogramma*, are nearly allied to one another and have many close similarities to the above; the main difference is that they have solitary basal ovules in the carpels, on account of which they were transferred to Phytolaccaceae by Pax (Engler & Prantl Nat. Pflzf. ed. 1, 3.1 b, 1-14, 33-51, 1889), but as in all other features they agree with *Mollugo* or *Pharnaceum*, such a separation seems unnatural. It is to be noted that H. Walter in his monograph on Phytolaccaceae (Pflzf. 4, 33, 1909) definitely excluded these genera from that family, a view later generally supported (cf. Pax & Hoffmann E. & P. ed. 2, 10.c, 189, 1934). Of the three genera *Polpoda* and *Adenogramma* appear to be derivatives from *Psammotropa*.

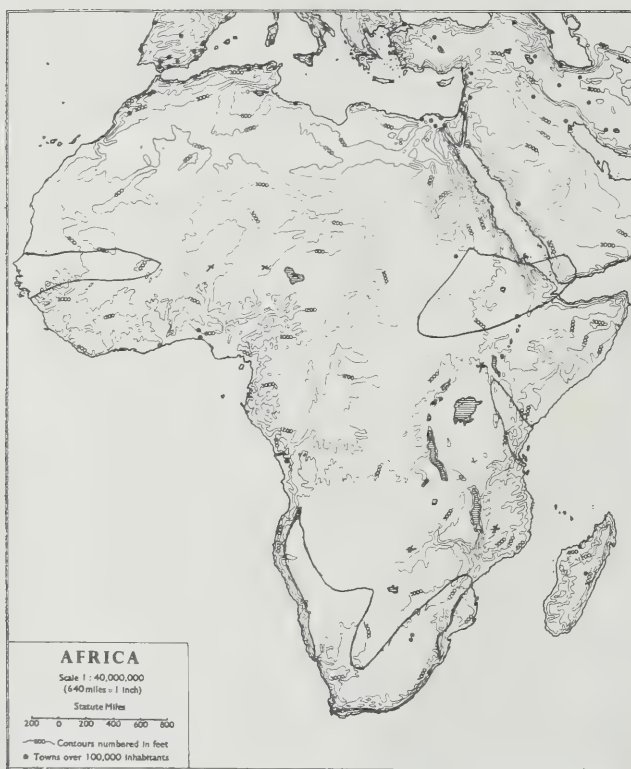
Glinus seems to be also a derivative from the same stock as *Mollugo* but along a distinct line. *Glischrothamnus* is derived from it.

Limeum, though often associated with *Psammotropa* and transferred with it, is so distinct in habit, inflorescence, flower and fruit, that no very close relationship seems probable. It stands nearest to *Gisekia* and the two may well be developments from a common original source.

Corbichonia is somewhat isolated though the Australian *Macarthuria* seems certainly derived from it.

GENERAL DISTRIBUTION.

Data on distribution have been taken from published accounts but have been checked as far as possible and often extended by reference to herbaria. As the plants are almost all rather inconspicuous and as much of the areas dealt with have by no means been fully explored botanically, it is most probable that the data available are incomplete and large allowances must be made for such uncertainties. Absence of records cannot be taken as definite evidence for absence of occurrence. Another factor adding to uncertainty is the fact that, especially in the tropics, a



1. General distribution of *Limeum* L. (adapted from Friedrich 1955).

number of species have become weeds and have spread as followers of man. The real range of these as indigenous plants is difficult to determine. Examples are *Mollugo verticillata* L. or *Glinus lotoides* L. In all that follows, allowance must be made for such considerations.

Taken as a whole the family is widespread and occurs throughout the tropics of both hemispheres. It extends to the warm temperate zone in Southern Africa and in Australia, but is generally absent from the temperate northern hemisphere except for one species in China and Japan and a few in the southern United States. The general distribution has a definite southern pattern. Of the 13 genera, 11 occur in Africa and no fewer than 6 are confined to its southern parts.

The most widespread genera are *Glinus* and *Mollugo*, both of which are pantropical and found in both Old and New Worlds. *Glinus* is strictly tropical and only extends to subtropical regions. *Mollugo* has species extending to the warmer temperate zone in both Africa and Australia, and one in China and Japan. *Glischrothamnus* is confined to Brazil.

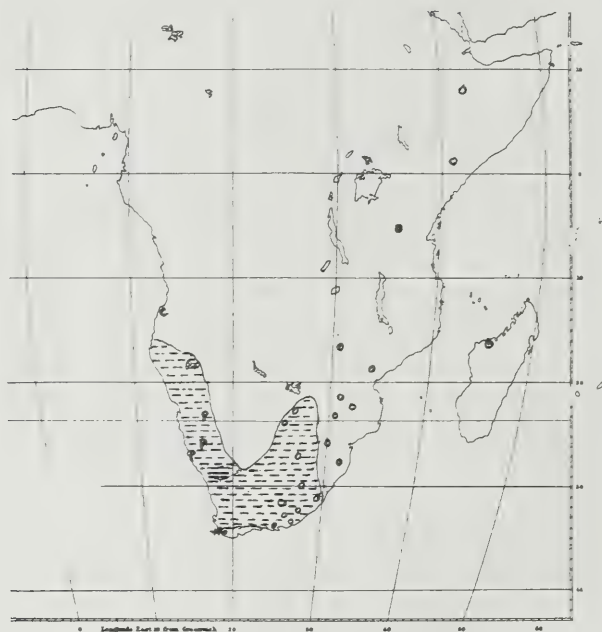
The three genera, *Corbichonia*, *Gisekia* and *Limeum*, are restricted to the tropics of the Old World. Of them *Gisekia* has the widest range. It extends throughout Tropical Africa, through Southern Arabia and Pakistan to India, Ceylon and the Malay region. In the south it extends to South West Africa, Transvaal and Natal. *Corbichonia* has a similar though slightly more restricted range. In the southern part of Africa it is recorded from South West Africa, Transvaal, and along the east coast to the south-east Cape Province. It is replaced in Australia by the allied *Macarthuria*.

The third genus *Limeum* (Map. 1) is more strictly African though a few species are reported from Southern Arabia and one from Pakistan. In Africa, as far as records go, the distribution is markedly discontinuous, with four main areas of occurrence and a few rather isolated records between them. The largest of these areas is in the south and extends from Angola and South West Africa through the Cape Province, Transvaal and Natal. The other areas are in Kenya and Tanganyika; in the southern Sudan, Abyssinia and south-west Arabia; and finally in the Senegal region of West Africa. As there are some isolated records of occurrence in intervening parts it is possible that increasing knowledge will result in a lessened discontinuity.

The remaining six genera are confined to Africa and almost to the southern half. All have species within the area of the Cape flora and *Adenogramma*, *Polpoda* and *Coelanthum* are confined to that region.

Of the others *Hypertelis* (Map 2) has the widest range and alone extends to the islands, having one species on Madagascar and one on St.

Helena. On the mainland it is found throughout the drier regions in the west, from South West Africa and Bechuanaland through the Cape Province to the western portions of the Transvaal and Orange Free State. There is one species with a very scattered range from the eastern Cape Province northwards to Abyssinia.



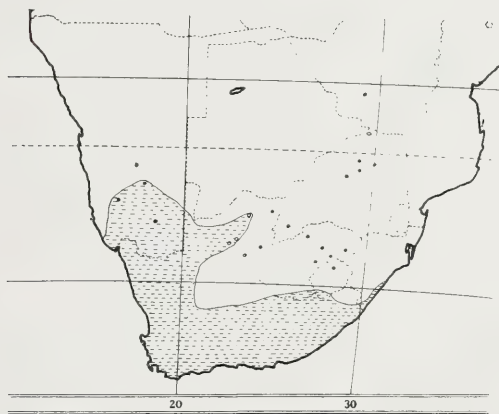
2. Distribution of *Hypertelis* E. Mey. ex Fenzl.

H. salsoloides --- : *spergulacea* === : *Bowkeriana* ○ : *suffruticosa* ○ :
arenicola ● : *trachysperma* + : *caespitosa* C : *angraepequanae* P.

Pharnaceum (Map. 3) is restricted to Southern Africa. Its range extends from South West Africa across the Cape Province and along the east coast as far as Durban. There are also scattered occurrences in Orange Free State, Basutoland, Transvaal and Southern Rhodesia.

Psamnotropha (Map 4) is more restricted but markedly discontinuous. The main area is in the eastern Cape Province, Natal, Basutoland, the eastern Orange Free State and Transvaal. There are smaller separated

areas in the south-west Cape Province, and isolated occurrences near Uitenhage, in Angola, and in Tanganyika and the Belgian Congo.



3. *Pharnaceum* L.

General range ---- : *P. brevicaule* ● : *viride* ○.



4. *Psammotropha* E. & Z. General distribution.

DISTRIBUTION OF SPECIES IN SOUTHERN AFRICA.

Gisekia, with two species and the monotypic *Corbichonia*, need no elaboration. Both are confined to the subtropical parts. *Glinus*, with three species, is similar. Two of the species are cosmopolitan, the third, *G. bainesii* (Oliv.) Pax, is restricted to a subtropical belt extending from Portuguese East Africa through Southern Rhodesia and the northern Transvaal to southern Angola. The species presumably arose there.

Mollugo has five species in Southern Africa: of these *M. nudicaulis* Lam. is a weed of the tropics that extends to South West Africa, Bechuanaland and the northern Transvaal; *M. cerviana* (L.) Ser. is a cosmopolitan weed of warmer regions which is scattered through the drier parts. The other three are ephemerals endemic to the western coastal belt: two, *M. pusilla* (Schltr.) Adamson and *namaquensis* Bolus, are rare or very local, the third, *M. tenella* Bolus, extends from Namaqualand to Swellendam. All three are specialized in relation to arid conditions and are probably recent developments.

Limeum has about 20 species. Of its separated areas of distribution the largest is that in the south. In that there is a maximum concentration of species in South West Africa. The discontinuity of generic range is not closely correlated with what would seem the phylogenetic features nor with specific distribution. For example, the section *Simonvillea*, which with its winged fruits might appear to be advanced, contains two species: of these *L. fenestratum* (Fenzl) Heimerl is spread over most of the southern area, but the other, *L. pterocarpum* (E. Mey.) Heimerl occurs in widely separated areas in South West Africa, in the Transvaal, and in Senegal. Again, the polymorphic species, *L. viscosum* (E. Mey.) Fenzl, is recorded from all the areas though in most it is rather rare. Other species are of very local occurrence. Few species occur within the area of the Cape flora proper: *L. africanum* L. is confined to the west coast belt between South West Africa and the Cape Peninsula; *L. aethiopicum* Burm. has a wide range across the margins of the karoo from South West Africa to the eastern Cape Province but is wanting from the south-western and southern coastal belts. *L. telephioides* E. Mey. ex Fenzl which is closely allied to *L. africanum* occurs in the eastern Cape.

Of the nine species of *Hypertelis* (Map 2) seven are of very local occurrence. The two on the islands are endemic there. On the mainland, two are local endemics in South West Africa, one on the Cape Flats. *H. arenicola* Sond. is found in the Cape Peninsula area and near Port Elizabeth. *H. spergulacea* E. Mey. ex Fenzl occurs in a limited area in the southern part of South West Africa and the north-west of the Cape Province, where it seems restricted to river beds. The other two are

wider ranging: *H. Bowkeriana* Sond. has a very scattered distribution on the east side of the continent from the eastern Cape to Abyssinia; *H. salsoioides* (Burch.) Adamson is common on suitable habitats through the drier parts of South Africa from Angola eastwards, also occurring in the Transvaal and in Southern Rhodesia. It is wanting on the mountains and from the moister parts of the coast belt.

Of the 25 species of *Pharnaceum* (Map 3), two extend outside the main area of distribution: *B. viride* Adamson on isolated elevations in the northern Cape Province and on the Zoutpansberg; and *P. brevicaulis* (DC) Bartl. (*P. Zeyheri* Sond.) in South West Africa, the northern Cape Province and especially in the grassveld in Orange Free State, Basutoland and Transvaal, with outliers in Southern Rhodesia. Within the main area two species are exceptional in being mountain plants: *P. serpyllifolium* L. f. on summits in the Cedarberg and Olifants River mountains, and *P. alpinum* Adamson on the southernmost Drakensberg. All the others are lowland species. Five occur in the region of the Cape flora: *P. aurantium* (DC) Druce, *dichotomum* L. f., *elongatum* (DC) Adamson, *lanatum* Bartl., and *lineare* L. f. Three others, *P. exiguum* Adamson, *incanum* L., and *microphyllum* L. f., are restricted to the west coastal belt. Five species, *P. albens* L. f., *confertum* (DC) E. & Z., *croceum* E. Mey. ex Fenzl, *gracile* Fenzl and *scleranthoides* Sond., occur in the western and northern karroo with a range from Namaqualand to southern Bechuanaland. *P. fluviale* E. & Z. and *trigonum* E. & Z. occur on the eastern karroo and the dry parts of the eastern coast belt. *P. Thunbergii* Adamson is an eastern species occurring on the coast from Knysna to Durban; it is closely allied to *P. cordifolium* L. found on sand dunes between the Cape Peninsula and Hermanus. The remaining species are local endemics.

The allied and derived genus *Coelanthum* has three species on the west coast belt at low altitudes.

Psammotropha has 11 species, of which two, *Ps. mucronata* (Thb.) Fenzl and *myriantha* Sond., are found on the higher ground between the eastern Cape Province and the valley of the Limpopo. Outlying stations for the former are known from Portuguese East Africa, for the latter from southern Angola and from Tanganyika and the Belgian Congo. *Ps. frigida* Schltr. is allied to *Ps. mucronata* but has a quite separated range: it occurs on summits of the Cedarberg, Gt. Winterhoek, the Worcester mountains, also on the Roggeveld escarpment and on the Swartberg (Map 5). Three species, all allied to *Ps. mucronata*, are local endemics on mountain summits on the Natal-Basutoland border. *Ps. marginata* (Thb.) Druce is endemic to a small area near Uitenhage. *Ps. diffusa* Adamson and *spicata* Adamson are local endemics on the Cedarberg and

Giftberg ranges respectively. The remaining two species occur on lower slopes and flats, *Ps. quadrangularis* (L. f.) Fenzl between Namaqualand and Worcester, also on the Witteberg and Swartberg but absent south of the Worcester valley; *Ps. anguina* Compton from the Clanwilliam, Ceres and Piketberg districts.



5. *Psammotropha* series *Mucronatae*.
Ps. mucronata ● : *myriantha* ○ : *frigida* +.

All the species of *Adenogramma* are confined to the area of the Cape flora: two, *A. glomerata* (L. f.) Druce and *Lichtensteiniana* (Ser.) Druce occur throughout, the others are more restricted, *A. sylvatica* (E. & Z.) Fenzl to the mountains along the south coast, *A. Mollugo* Reichb. to the west coastal plain, the others very local. The species of *Polpoda* occur on lower slopes and flats: *P. capensis* Presl between Clanwilliam and Mossel Bay, *P. stipularis* (Leighton) Adamson in the Clanwilliam, Ceres and Worcester districts.

RELATIONSHIPS WITH THE CAPE FLORA.

If those genera which are confined to tropical or subtropical zones are disregarded, all the others have species in the strict area of the Cape flora and some, *Adenogramma*, *Coelanthum* and *Polpoda*, are confined to it.

In analysing the Cape Flora, Levyns (1952) has found that if the number of species in a genus occurring in the various divisions covered by the flora is counted, there is, for the characteristic members of the flora, a maximum number in or about the Caledon or Worcester divisions and a decrease in numbers to the north and to the east. The maximum occurs where the mountain ranges along the west coast and those along the south coast come together. This is the region of greatest rainfall and this concentration of species there is correlated with the drying of the climate.

If this scheme is applied to these genera, it is found that there is complete agreement in the case of *Adenogramma* and *Polpoda* but not for the others. The figures for *Hypertelis* and *Limeum* are quite different, for *Pharnaceum* there is a maximum in the north, in the Clanwilliam division, and a decrease to the south and east. For *Psammotropha* the number of species is too small for the scheme to be applicable. This genus has its maximum in what Weimareck (1941) has termed the Drakensberg centre which is outside the area dealt with, though there is an indication of a secondary maximum in the Clanwilliam division. The actual figures are:

TABLE I.

	Adenogramma and Polpoda	Pharnaceum total	Selected	Limeum	Hypertelis	Psammotropha
Total ..	12	27	9	14	7	11
Division						
S.W.A. ..	1	7	1	11	4	—
Namaqualand ..	5	13	8	7	2	1
Clanwilliam ..	6	15	9	2	1	4
Ceres ..	4	8	5	—	—	2
Paarl ..	4	6	5	1	—	—
Caledon ..	7	6	4	1	—	—
Worcester ..	8	6	4	1	1	2
Swellendam ..	5	5	3	6	1	—
Riversdale ..	3	6	3	—	—	—
Mossel Bay ..	1	3	2	—	1	—
George ..	1	1	1	—	—	—
Knysna ..	2	4	1	—	—	—
Humansdorp ..	1	3	1	—	—	—
Albany ..	1	5	2	1	2	—

From the table, it would seem that *Adenogramma* and *Polpoda* are true members of the Cape flora but that *Hypertelis* and *Limeum* are not. The divergence from expectation in the case of *Pharnaceum* should not be overstressed. The figures fit into the scheme except for a shift of the maximum to the north. An explanation for this may be obtained from the fact that the species of this genus, with very few exceptions, are plants of low ground and especially characteristic of the drier parts of the Cape floral area. Conditions favourable to them are especially extensive in the north. On the other hand, the plants on which Levyns' figures were based are all mountain plants, that is plants with a higher moisture requirement than these. As it might be objected that the figures for *Pharnaceum* include several species that only occur in the Cape area in the north and that have their main range outside, a separate analysis was made based on those species only which are confined to the Cape area. The figures so obtained exhibit exactly the same proportions. From this it may be taken that the genus really belongs to the Cape flora though to the drier parts of it. This conclusion is supported by the existence in it of one true mountain-top species, and by the fact that the small derivative genus, *Coelanthum*, is confined to the dry western coastal belt.

The divergencies in the cases of *Hypertelis* and *Limeum* are such that they cannot be fitted into the scheme. *Hypertelis* has only two species really within the area. Both are very local and found in specialized habitats. The rest are karoo plants occurring in dry areas in some of the divisions. In the case of *Limeum*, *L. africanum* L. is confined to the western coastal belt, *L. aethiopicum* Burm. occurs on the karoo margin and only enters the area proper in the dry regions near Uitenhage. A third species, *L. subnudum* Friedr., is a local endemic in the Olifants River valley. In both cases the patterns suggest invasion from the north. The same seems to be the case with the few species of *Mollugo* which occur on the western coastal belt.

In contrast to these, the species of *Psammotropha* are mountain plants. Of those found within the Cape area, *Ps. frigida* is restricted to summits towards the northern boundary of the area. It is allied to *Ps. mucronata* found in the south-east, and appears as a relic that has become separated by geographical isolation. The others are local endemics except for *Ps. quadrangularis* and *anguina* which appear to be modifications in relation to drier conditions. The distribution can best be explained in being that of a relic from a once more extensive Cape flora.

Summing up conclusions drawn from such analyses, it appears that *Adenogramma*, *Polpoda*, some species of *Pharnaceum*, and probably some of *Psammotropha* belong to the Cape flora proper, but that *Limeum*, *Mollugo* and *Hypertelis* do not.

GENERAL CONSIDERATIONS.

All the genera have the characteristics of old and well established ones. Most of those in the tropics have wide ranges. Several, including most of those represented in Southern Africa exhibit some discontinuity in range which indicates a restriction of their one-time extent. The cause of such restriction of range must be looked for in environmental changes, either physical, climatic or both, which have occurred. The occurrence of such changes in the southern part of the continent have been discussed by Weimarck (1939-1941) and by Levyns (1952-1954), and only the merest outline is called for here. Southern Africa has been a land surface, for the most part stable, at any rate since later Cretaceous times, that is, since the appearance of dominance of the angiosperms. The Cape mountains, which provide the main habitat for the characteristic Cape flora, have not undergone any major change during this period. Again, the karoo area on their inland side has been a land surface for at least as long. It is on the coastal belts that there have been changes in plant habitats which have been the result of alterations in the relative levels of land and sea. During Cretaceous and early Tertiary times much of the present belt was submerged. In later times, Pleistocene, there seems to have been a considerable elevation of the land that produced extensions that included much or possibly all of the present Agulhas Bank. Such extension of land habitats would have opened up paths for plant movements both east and west. Much of this land was again submerged and though in the Quaternary there was again elevation, this was less extensive than the older phase. During these changes there must have been changes in the habitats for coastal and lowland species and the appearance of some new ones. It appears also that in the Cape flora region there are two kinds of habitat, the mountains which are old and stable and have been affected by changes of climate only, and the more recent ones on the coastal plains. Even the latter are of two kinds, those that have existed since the Pleistocene uplift and those that date from the recent raising of the land.

Habitat changes resulting from such changes in level provide a clue to the cause of discontinuous distribution in some lowland species (Levyns 1954). For example, *Hypertelis arenicola* Sond. has stations at the Cape and near Port Elizabeth but nowhere between. This appears to be a species that became established before the later Tertiary depression during which it disappeared along most of the south coast. A parallel case, though the survivors have become specifically distinct, is that of *Pharnaceum cordifolium* and *Thunbergii*.

In Tropical and North Africa greater changes seem to have taken place. In Eocene times the Tethys Sea which separated Africa from the northern lands was much extended and covered much of what is now the Sahara. It had, further, an extension that reached the Gulf of Guinea (Stern 1932; Gregory 1929). At a later period, from the Oligocene onwards, this sea underwent contraction and became separated as a land-locked sea now represented by the Mediterranean. It was about the Oligocene era that land connection between Africa and southern Asia was established which presumably allowed the spread of *Limeum* and others to southern Arabia.

CHANGES OF CLIMATE.

There are many sources of evidence to show that there have been considerable changes in the climate of Africa and especially of southern Africa during the period when angiosperma have been dominant, but these need no discussion here. In the south and especially in the region of the Cape flora, such changes and their influence on distribution have been discussed by Weimareck (1941) and by Levyns (1938, 1952) and need no elaboration. The general conclusion is that the present is a dry or drying phase.

In the region inland of the Cape mountains, there has been, in addition to minor fluctuations, a major climatic change which has resulted in the extermination of the Cape flora and its replacement by the more recent and more drought-resistant flora of the karoo. This was first discussed by Marloth (1898) and has been investigated in some detail by Levyns (1938). While over large areas this replacement of floras has been complete, there are some isolated mountains and elevations on which the old flora has been able to maintain itself either wholly or partially. Such elevations form islands of Cape flora which are surrounded by the younger flora. Their altitude is sufficient to maintain a climate of a degree of moisture sufficient for the continued existence of the old flora.

The drying of the climate which brought about these changes and which seems to be still in progress, must have commenced at a time sufficiently distant to permit of the development of endemic species on some of the island ranges (Levyns *l.c.*).

Further north, in the Kalahari region, there existed severe desert conditions at an earlier period. This desert, which produced deep and extensive deposits of sand, covered Bechuanaland and extended over much of Southern Rhodesia and the northern Transvaal. It appears to have reached its maximum intensity about the Pliocene or early Pleistocene epoch. At the present time the region has a much ameliorated

climate that is far from extremely arid. Even the so-called "Kalahari Desert" owes its reputation to the almost complete absence of surface waters. It appears that in Southern Africa the subtropical desert belt has altered in position and is now further south than in the past and that there has been a climatic change towards aridity which has progressed from north to south.

A climatic change such as this would be neither sudden nor quite continuous and the effects on the plants of the region would be complex. Without entering on any details, the ultimate result would be that two kinds of habitat would be formed, firstly old and relatively stable ones in which elevation or some other factor retained sufficient moisture to allow the continued existence of the older flora, and secondly, plains and lower levels where the full effects were felt and only plants of the newer arid flora could exist.

ENVIRONMENT CHANGES AND DISTRIBUTION.

The distribution patterns of the genera fall into two groups, the one tropical the other more temperate. Of the former, *Corbichonia*, *Gisekia*, *Glinus* and *Mollugo* in Africa appear to have been prevented from any extension to the northern regions by the Tethys Sea. In the south the old Kalahari Desert seems to have been a complete barrier. Following the amelioration of the climate there, there was a southward migration which extended as far as the northern Transvaal and further along the east coast. This movement was accompanied by some species differentiation; for example, such a species as *Glinus Bainesii* presumably arose during this phase.

In the north the diminution of the Tethys Sea permitted spread to Arabia and eastwards though *Mollugo* is the only genus which has reached the warmer temperate zone.

In the south, where it has also extended, the species are confined to the more recent types of habitat, and appear to have arisen in relation to the drying of the climate. All seem relatively recent, the spread of *M. cerviana* over the karoo especially so.

Among the tropical genera *Limeum* has a distinct type of distribution in which the existing range is a mere fraction of what it once must have been. The break-up of range must have begun after the main lines of evolution of the species had taken place. Of the existing areas the largest, in the south, would seem to have become isolated by the Tertiary Kalahari Desert. Even to-day the greater part of Bechuanaland is a region where there are no records of occurrence. Further, *L. dinteri* Schellenb. is recorded from South West Africa and from the northern Transvaal but

not between. The widespread *L. viscosum* (Gay) Fenzl is represented in South West Africa on the one hand and in Southern Rhodesia and the Transvaal on the other, by distinct subspecies.

In the north, the separation of the Senegal area can be explained by an early Tertiary depression in extension of the Tethys Sea, though this would imply that establishment and differentiation already existed in Cretaceous times. In this connection, it may be noted that there is a similar gap in range between Angola and West Africa in the genus *Aizoon* (Adamson 1959). The discontinuities in East Africa are explicable on climatic changes in mid-Tertiary times and later.

Though the genus seems an old one which is largely retreating, it does show signs of species differentiation, notably in the Angola-South West Africa region, where there are a number of local endemic species. Some of these occur throughout the region, such as *Limeum myosotis* H. Walt.; others are very much restricted, e.g. *L. arenicolum* Schellb.

Of the species that occur within the Cape flora, *L. aethiopicum* Burm. seems an invader from the adjacent karoo flora, *L. africanum* L., which is confined to the younger west coast, a rather recent modification.

Of the more temperate genera, *Hypertelis* has the widest range and is the only one not confined to the continent. It has endemic species on Madagascar and on St. Helena. On the mainland all but two of the species have very much restricted ranges. Two are local endemics in South West Africa, one is endemic to the Cape Flats, *H. arenicola* Sond. on the south coast has already been noted, *H. spegulacea* E. Mey. ex Fenzl occupies a limited area in the southern part of South West Africa and the north-west Cape Province. It is confined to river beds and may well be a survivor from a time when the climate was less arid.

H. Bowkeriana Sond. has a wider but very discontinuous range from the eastern Cape Province to Abyssinia. The Madagascan species *H. suffruticosa* (Baker) Adamson is closely allied and would seem to have been differentiated by isolation. Its origin must date back to the time when Madagascar was united to the mainland and hence be similar to that of other Cape genera which have species on the island (cf. Levyns 1952; Weimarek 1939, 1942).

In contrast, the remaining species, *H. salsoloides* (Burch.) Adamson has a wider and continuous range over the drier parts of South Africa. It is a variable species which is confined to the newer types of habitat and is wanting on the Cape mountains. It would appear to have spread subsequent to the drying of the climate. Alone among the species it has none of the features of a relic.

Pharnaceum has a continuous range in the south with two species more or less separated. One of these, *P. viride* Adamson, occurs on

separated elevations in the north-west Cape Province and on the widely separated Zoutpansberg. The species is allied to the more widespread *P. aurantium* (DC) Druce and seems to be a relic surviving in a few relatively protected sites. The other, *P. brevicaule* (DC) Bartl., which is known from South West Africa, from scattered stations in the north-west Cape, from many in the uplands of Basutoland, the eastern Orange Free State and Transvaal, and a few in Southern Rhodesia as far north as Bulawayo, is a species rather specialized in habit and not very closely allied to any other. The distribution suggests that the generic range was at one time wider and that these two are survivors which have withstood a drying climate which has eliminated others, and that they have become modified in isolation.

Of the other species a number have been shown to be true if rather xerophytic members of the Cape flora which occur on the lower mountain slopes or their immediate neighbourhood, that is on the older more stable type of habitat. In contrast, a number of species are found to-day only on the younger habitats, the karoo or the western coastal belt. The karoo species especially, such as *P. confertum croceum*, or *scleranthoides*, are specialized in a number of features and would seem to be relatively recent differentiations correlated with the drying climate. If so, the generic range would be evidently discontinuous though the gap between the two persisting relics, *P. brevicaule* and *viride*, has become reduced by the differentiation and spread of the karoo species.

Within the genus the position of *P. serpyllifolium* L. f. is unique. It is confined to mountain summits in the Cedarberg and some associated ranges. In structure it would seem a primitive species which in certain features approaches *Mollugo*. At present it appears to be a relic which has survived drying of the climate. It is a tempting hypothesis that it is a survival from a moisture-demanding ancestor, the other descendants of which have become xerophilous and inhabit lower levels, but there is no evidence in support.

It was noted earlier that *Pharnaceum* and *Mollugo* are closely allied and apparently derived from a common ancestor. The generic separation must have taken place at a remote period as at present the ranges of the two are quite separate and only overlap where recently evolved species of *Mollugo* have penetrated southwards. All the species of *Pharnaceum* are in the more temperate regions in the south where their range has become restricted by drying climate. What seem to be the least specialized species are those within the area of the Cape flora. There is no evidence for any southward movement in the genus.

The rather scattered and discontinuous distribution of *Psammotropha*

represents a mere fraction of its one-time extent. Some notion of what it was is to be got from the existing stations in Angola, the Belgian Congo, and in Portuguese East Africa. Most of the species are mountain plants that demand a cool climate without prolonged drought periods. The restricted range is attributable in the main to drying of the climate which must have commenced at least by the middle Tertiary period. The more extensive range at the present time in the east is attributable to the lesser degree of drying that has occurred there. The species in the western Cape are very local in occurrence and appear to be survivors from previous less arid conditions. Two species here, however, *Ps. quadrangularis* L. f. and *anguina* Compton, occur on lower mountain slopes and flats and seem to be more recent differentiations in relation to drier conditions. As the former is found on some of the isolated ranges surrounded by the karoo, their differentiation must date back to a time previous to the extreme drying which led to the disappearance of so much of the old flora. Differentiation of species in more recent times seems to have occurred on the higher summits of the Drakensberg where there are derived species of local occurrence which have not yet spread far from their point of origin.

Adenogramma and *Polpoda* which are allied to *Psammotropha* are both restricted to the region of the Cape flora. *Polpoda* is allied to and possibly derived from some of the species of *Psammotropha*. If so, this differentiation must have taken place sufficiently long ago to allow *P. capensis* Presl to attain a wide distribution through the Cape floral area.

Adenogramma has a range coextensive with the main area of the Cape flora. In it the perennial species appear to be the more primitive. *A. lichtensteiniana* (Ser.) Druce, which is somewhat drought resistant, has a wide range on the mountains, but *A. sylvatica* (E. & Z.) Fenzl is confined to moist kloofs along the south coast and seems to be a species surviving from conditions of greater moisture. Such restriction seems to have been carried even further in the local species *A. rigida* (Bartl.) Sond. and *A. teretifolia* (Thunb.) Adamson which have very limited ranges on the coastal plain. The more specialized annual species appear to be more recent differentiations some of which have spread widely on the younger habitats.

There is no satisfactory evidence bearing on the origination of the genus though many of the species both perennial and annual show similarities to species of *Psammotropha*.

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